Title

Mass coral bleaching causes biotic homogenization of reef fish assemblages

Running head

Coral bleaching causes biotic homogenisation

Authors

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Abstract

Global climate change is altering the composition of ecosystems due to non-random species turnover, typically characterized by the loss of specialist species and increasing similarity of biological communities across spatial scales. As anthropogenic disturbances continue to alter species composition globally, there is a growing need to identify how species responses influence the establishment of distinct assemblages such that management actions may be appropriately assigned. Here, we use trait-based analyses to compare temporal changes in five complementary indices of reef fish assemblage structure among six taxonomically distinct coral reef habitats exposed to a system-wide thermal stress event. Our results revealed increased taxonomic and functional similarity of previously distinct reef fish assemblages following mass coral bleaching, with changes characterized by subtle but significant shifts in dominant fish taxa towards small-bodied, algal-farming habitat generalists. Furthermore, whilst the taxonomic or functional richness of fish assemblages did not change across all habitats, an increase in functional originality indicated an overall loss of functional redundancy. We also found that pre-bleaching coral composition better predicted changes in fish assemblage structure than the magnitude of coral loss. These results emphasise how measures of alpha diversity can mask important changes in the structure and functioning of ecosystems as assemblages reorganize. Our findings also highlight the role of coral species composition in structuring communities and influencing the diversity of responses of reef fishes to disturbance. As new coral species configurations emerge, their desirability will hinge upon the organisation of associated species and their capacity to maintain key ecological processes in spite of ongoing disturbances.

Introduction

Pervasive anthropogenic disturbances have altered the structure of ecological communities and the functioning of ecosystems, primarily through habitat change, exploitation, and pollution (Cardinale et al., 2012; Ellis et al., 2013). Species extirpations and introductions modify the composition of local assemblages, often reducing biodiversity within (alpha diversity; α), and among (beta diversity; β) communities (Dornelas et al., 2014; McGill, Dornelas, Gotelli, & Magurran, 2015). This resulting species turnover typically occurs non-randomly, often varying with organism characteristics such as body-size, physiology, habitat specialisation and trophic level (McKinney, 1997; Graham et al., 2011). Long-term observations of trait-filtering across groups such as plants, mammals, birds, and fishes, indicate declines in specialist species in response to past and current global changes (Clavel, Julliard, & Devictor, 2011). These declines have caused increasing taxonomic and functional similarity (i.e., biotic homogenization) at the community level, threatening ecosystem functioning and resilience (Elmqvist et al., 2003; Olden, LeRoy Poff, Douglas, Douglas, & Fausch, 2004; Clavel et al., 2011). Two facets of species biodiversity are expected to confer ecosystem resilience to disturbance during ecological reorganization: (i) functional redundancy (the capacity of one or more species to functionally compensate for the loss of another), and (ii) response diversity (the diversity of species responses to environmental change within functional groups such that functions may be maintained) (Walker, 1992; Elmqvist et al., 2003; Nyström, 2006; Nash, Graham, Jennings, Wilson, & Bellwood, 2016).

We focus on coral reefs, one of the world’s most biodiverse but threatened ecosystems (Hughes et al., 2017), to assess how species response diversity to disturbance influences ecological organisation across scales (within and across distinct reef habitats). Climate-induced coral bleaching represents the foremost threat to coral reefs, with severe thermal stress events causing widespread coral loss, altering the structure of coral reef habitats and the composition of reef-associated species (Graham et al. 2006; Hoegh-Guldberg et al. 2007; Pratchett, Hoey, Wilson, Messmer, & Graham, 2011). Mass bleaching has been shown to cause local extirpations of coral reef fishes with corresponding declines in fish species richness and total abundance (Wilson, Graham, Pratchett, Jones, & Polunin, 2006). However, reef fish and coral species responses to extreme thermal stress can be highly variable (Wilson et al., 2006; McClanahan, 2017), likely due to inherent differences in the response of corals to ocean warming (Pandolfi, Connolly, Marshall, & Cohen, 2011), as well as differential trait-vulnerability of fish species associated with distinct coral habitats (Graham et al., 2011; Richardson, Graham, Pratchett, & Hoey, 2017). Sustained ocean-warming increases the risk of further mass bleaching events (Hughes et al., 2017). However, how distinct species assemblages will vary in their susceptibility to change is not well understood.

There is a growing need to understand how different configurations of species on coral reefs respond to disturbance and contribute to ecosystem function (Graham, Cinner, Norström, & Nyström, 2014), such that coral reef management efforts may be allocated appropriately. Previously unseen disturbance-mediated configurations of species are increasingly reported on coral reefs (Pandolfi et al., 2011; Pratchett, Trapon, Berumen, & Chong-Seng, 2011; Bento, Hoey, Bauman, Feary, & Burt, 2016). Increasing selective disturbances are causing shifts in coral species dominance, as well as overall declines in species diversity (Aronson, Macintyre, Wapnick, & O'Neill, 2004; Pratchett et al., 2011; Alvarez-Filip, Carricart-Ganivet, Horta-Puga, & Iglesias-Prieto, 2013). These altered configurations are predicted to persist into the future due to taxa specific responses to perturbations, recovery potential, and capacity for rapid adaptation under projected climatic changes of global warming and ocean acidification (Pandolfi et al., 2011). The biological and physical structure of coral reef habitats exerts considerable influence over the structure of reef fish assemblages (Luckhurst & Luckhurst, 1978; Roberts & Ormond, 1987; Friedlander & Parrish, 1998; Darling et al., 2017), important ecosystem processes such as herbivory (Cvitanovic & Hoey, 2010), predator-prey dynamics (Hempson et al. 2017), and other intraspecific and interspecific fish species interactions (Kok, Graham, & Hoogenboom, 2016). Indeed, shifts in coral assemblage composition have also shaped novel reef fish assemblages, where despite regaining pre-disturbance coral cover in some instances, populations of some fish species show little evidence of recovery generations later (Bellwood et al., 2012; Berumen & Pratchett, 2006).

Here we assess the susceptibility of distinct species configurations to the impacts of mass coral bleaching to elucidate the influence of pre-disturbance coral species composition on the resilience of tropical reefs, and consider the effects of response diversity on ecological organisation. Specifically, we use trait-based approaches to compare the taxonomic and functional structure of reef fish assemblages among six taxonomically distinct coral reef habitats seven months before, during, and six months after severe coral bleaching at Lizard Island, in the northern Great Barrier Reef, Australia.

Materials and methods

Study sites

Lizard Island (14°41′S, 145°27′E) is a granitic mid-shelf island located 30 km offshore from mainland Australia, in the northern section of the Great Barrier Reef. The island is largely encircled by well-developed fringing reefs and an extensive lagoonal system of patch reefs.

In 2016, the northern Great Barrier Reef (including Lizard Island) was subject to extreme temperature stress, with peak daily sea surface temperatures reaching 32.8 °C in February 2016, and a high thermal load of >8 degree heating weeks (°C-weeks) by April 2016, triggering mass coral bleaching (Hughes et al., 2017).

Benthic and fish assemblages were surveyed at 16 sites on the leeward side of Lizard Island seven months before, during and approximately six months after the bleaching event, in September 2015, April 2016, and October 2016 respectively. Sites were randomly selected in September 2015 within the following constraints: there was >250 m x 5 m of contiguous reef, adjacent sites were separated by >500 m, and were protected from prevailing south-east swell with comparable water clarity and geomorphology.

Assessment of benthic and fish assemblages

Benthic and fish assemblages were surveyed along six replicate 30 m transects at each site, positioned on shallow (<6 m) reef edges and parallel to the reef–sand interface in each time-period. Transect position was initially random in September 2015, and the starting position of individual transects were subsequently identified visually within the same approximate area (within 1–2 m) by the same surveyors (LR and JE) for the following survey periods.

The point-intercept method was used to quantify benthic composition and coral bleaching extent, recording the substrate immediately below the transect tape at 25 cm intervals (120 points per transect). Substratum categories were hard (scleractinian) and soft (alcyonacean) corals recorded to genus (or species where possible) and growth form, ‘other sessile invertebrates’ (primarily sponges, giant clams, and ascidians), macroalgae, erect crustose coralline algae, ‘dead substrate’ (dead coral and pavement), rubble, and sand. Coral bleaching was estimated for live coral tissue that lay beneath the survey points (recorded in April and October 2016). A 6-point colour saturation scale based on the CoralWatch colour reference card was used *in situ* to minimise subjective assessment of bleaching state (Siebeck, Marshall, Klüter, & Hoegh-Guldberg, 2006). Coral tissue with saturation scores of 1–2 was considered bleached and 3–6 unbleached to provide an estimate of the percent cover of bleached coral along each transect. No explicit account was made of bleaching variation within coral colonies.

The species identity, abundance, and body-size (total length; TL, to the nearest cm) of all non-cryptic fishes were recorded on transects. Larger, more mobile species (>10 cm TL) were counted as transects were laid in a 5 m wide belt, and smaller fishes (≤10 cm) were surveyed in a 1 m belt on the return pass. All fish surveys were conducted by a single observer (JE) and the fish abundances standardised per 150 m^2. Fish species were classified into functional entities according to six ecological and morphological species traits: diet, mean observed body-size (TL; 10 cm size categories), social grouping, mobility within/between reefs, time when active, and position in the water column (following Mouillot, Graham, Villéger, Mason, & Bellwood, 2013) (Table S1). Body-size was estimated with the mean observed sizes of each species in the September 2015 and October 2016 surveys, unless species were observed only in April 2016 whereby mean size was estimated for that period only.

Data analysis

Benthic composition

Pre-bleaching variation in benthic composition among sites was visualized with non-metric Multidimensional Scaling (nMDS) based on a Bray-Curtis similarity matrix of square root transformed transect level data. Groupings identified with nMDS were tested using a two-way nested PERMANOVA (maximum permutations = 9999), using habitat grouping (fixed) and site (random) as factors. One-way unrestricted permutations of raw data was used for pairwise comparisons between habitats to allow testing of sufficient permutations, followed by percentage similarity analysis (SIMPER) to identify substratum categories consistently contributing to mean similarity within or dissimilarity between habitats (with similarity/dissimilarity test ratio of >4.0 or 2.0, respectively (Clarke & Warwick, 2001); Table S2). The percentage of total coral cover (hard and soft coral) that bleached was compared among habitats using linear mixed-effects analyses (with lme in *nlme*; R Development Core Team 2016), using habitat as a fixed effect and site as a random effect. Changes in total percentage coral cover (hard and soft coral) among habitats following the bleaching event were assessed with habitat and period (and their interaction) as fixed effects and site (random effect). *Post hoc* multiple comparison Tukey tests were used to identify where differences occurred.

Fish assemblage structure

Trait-based functional diversity was calculated by constructing a principal coordinates analysis (PCoA) of species pairs based on trait combinations and a Gower distance matrix, with a square root correction for negative eigenvectors (Legendre & Legendre, 1998). Four synthetic PCoA axes summarizing species distribution within functional trait space were then combined with species abundances to calculate three complementary indices of functional diversity for each transect in all periods: functional richness, functional dispersion, and functional originality (Mouillot et al., 2013; Maire, Grenouillet, Brosse, & Villéger, 2015). Functional richness is calculated as the proportional convex hull volume occupied by a species assemblage in multidimensional functional space (PCoA), and represents the range of unique trait combinations. Functional dispersion measures the abundance-weighted deviation of species traits in an assemblage from the centroid of all species in functional space, and reflects the assemblage spread, or variability, of species traits (Laliberté & Legendre, 2010). Functional originality is calculated as the mean pairwise distance between species in an assemblage where greater mean distance infers greater functional originality and isolation of species in functional space. Functional richness and functional dispersion provide presence-absence and abundance-weighted facets of functional diversity respectively, whilst functional originality indicates how changes in species abundances modify the functional redundancy among species (Mouillot et al., 2013). Variation in the functional structure of fish assemblages through time was assessed using community-weighted transect means (CWM) of assemblages in each habitat before, during and after bleaching, measured using the four PCoA axes combined with species abundance values.

Linear mixed-effects models were used to assess variation in the structure of fish assemblages in two distinct analyses, both (i) within each habitat across time-periods, and (ii) among habitats within each time-period. First, within-habitat variation in fish assemblage structure over time was assessed using habitat type, time-period, and their interaction fitted as fixed effects, site as a random effect, and planned comparisons used post hoc to identify where changes occurred. Second, among-habitat variation in assemblage structure was assessed in each time-period using habitat (fixed effect), site (random effect), and Tukey multiple comparisons *post hoc* to identify where differences occurred (with *multcomp*). Count data models of fish species richness and total fish abundance were fit with Poisson, and negative binomial distributions respectively, to accommodate non-stable variances and alternative exponential residual distributions (with glmer in *lme4*). Continuous measures of fish functional richness, functional dispersion, functional originality, and the CWM values for all four PCoA axes were normally distributed and were fitted with a Gaussian residual structure (with lme in *nlme*). Functional originality was fitted with a constant variance structure to allow for existing heterogeneity of variance. Inter-habitat variation in the taxonomic composition of fish assemblages was tested using two-way nested PERMANOVAs for each period (maximum permutations = 9999) on square root transformed data, with habitat (fixed factor) and site (random factor). Due to limited available permutations, Monte Carlo sampling was used to estimate *post hoc* pairwise comparisons (Anderson & Robinson, 2003).

The relative influence of coral loss on variation in fish species richness, total abundance, functional richness, functional dispersion and functional originality was estimated using mixed effects multiple linear regression (total coral cover %, time-period, habitat, and period-habitat interaction as fixed effects, and site as a random effect). Information-theoretic model selection based on AICc ranking (ΔAICc values <2) was used to quantify model uncertainty and the relative importance of each explanatory variable (all predictors had Spearman's correlation coefficients <0.4 and variance inflation factors, $GVIF^{(1/(2*df))}$ <3) (Burnham & Anderson, 2002). Models within ΔAICc <2 with the fewest degrees of freedom were considered the most parsimonious.

Exploratory graphical analyses of residuals were used to confirm that assumptions of homogeneity of variance, normality, and independence were met for all linear regression modelling, and generalised mixed effects models fit with Poisson or negative binomial distributions were tested for overdispersion. Multivariate analyses of benthic composition were performed in Primer v6 with +PERMANOVA add on package (Clarke & Warwick, 2001). All other analyses were performed in R (R Development Core Team 2016), and the packages *ape*, *cluster*, *geometry*, *polycor*, *rcdd*, *vegan*, and the function *FDchange* in *FD*.

Results

Benthic composition

Analyses of benthic composition across the 16 study sites revealed six major habitat groupings characterised by a disproportionate cover (25–54% of the total benthos) of (i) *Porites cylindrica* (hereafter branching *Porites*), (ii) massive *Porites* (mostly *Porites lutea*), (iii) *Pocillopora damicornis* (hereafter *Pocillopora*), (iv) soft coral, (v) mixed coral assemblages, and (vi) dead coral and macroalgae (<10% coral cover, hereafter degraded) (Fig. S1; PERMANOVA: Pseudo-$F = 8.09$, $P = 0.0001$, all pairwise comparisons $P \leq 0.0002$; Table S2 and S3). These 'degraded' sites were subject to localised disturbance from recent cyclones and predation by crown-of-thorns starfish that caused acute coral loss on those reefs. Four of the six broad habitat groupings were represented by three sites, while massive *Porites* and *Pocillopora* habitats were represented by two and one site(s), respectively. Prior to the bleaching event, total coral cover (hard and soft coral) was similar among surveyed coral habitats (mean ± SE: 50.4 ± 3.6), which all had significantly greater cover of live coral than degraded habitats (Tukey, all $P < 0.002$). Coral bleaching was widespread across surveyed sites in April 2016 affecting 51% of total coral cover (31 out of 36 coral taxa; Table S4), and did not vary significantly among habitats (percentage bleached of total coral cover; all pairwise comparisons, $P > 0.05$) (Table 1). However, the mortality of corals following the bleaching event varied among taxa (primarily soft coral, branching *Porites* and *Acropora*; Fig. S2), causing significant declines in coral cover by October 2016 in just three habitats: soft coral (31%), mixed coral (18%), and branching *Porites* (15%) habitats (Table 2; Fig. 1; Table S5). Coral cover remained higher in all coral habitats relative to the degraded habitat in October 2016 (Tukey, all *P* <0.01).

Table 1 Mean ± SE percent cover of benthic composition and coral bleaching extent within habitats from September 2015 to October 2016.

Habitat	September 2015	April 2016			October 2016	Change in coral cover (Sept. 2015–Oct. 2016)
	Total coral cover	Total bleached coral cover	Percent bleached of total coral cover	Percent bleached of dominant coral taxa	Total coral cover	
Branching *Porites*	57.13 ± 2.79	21.81 ± 1.80	43.73 ± 2.92	45.86 ± 4.39	42.08 ± 2.30	-15.01 ± 3.39
Degraded	10.46 ± 1.80	7.04 ± 0.96	59.80 ± 4.74	-	14.63 ± 1.87	4.12 ± 3.39
Massive *Porites*	49.37 ± 2.81	23.82 ± 1.55	47.61 ± 4.06	46.96 ± 4.58	46.60 ± 3.19	-2.78 ± 4.15
Mixed coral	46.63 ± 3.07	15.03 ± 1.65	45.72 ± 4.18	-	29.03 ± 2.43	-17.88 ± 3.05
Pocillopora	39.31 ± 6.01	25.69 ± 1.73	56.68 ± 4.64	57.86 ± 4.58	35.83 ± 3.41	-3.47 ± 5.87
Soft coral	59.49 ± 1.93	27.27 ± 2.32	67.15 ± 3.23	67.95 ± 3.58	28.56 ± 2.65	-30.93 ± 3.39

Due to differential coral loss, coral cover varied among coral habitats following the bleaching, with cover in mixed coral, and soft coral habitats significantly lower than branching- and massive- *Porites* habitats, and *Pocillopora* habitat remaining intermediate (Tukey, all *P* <0.02).

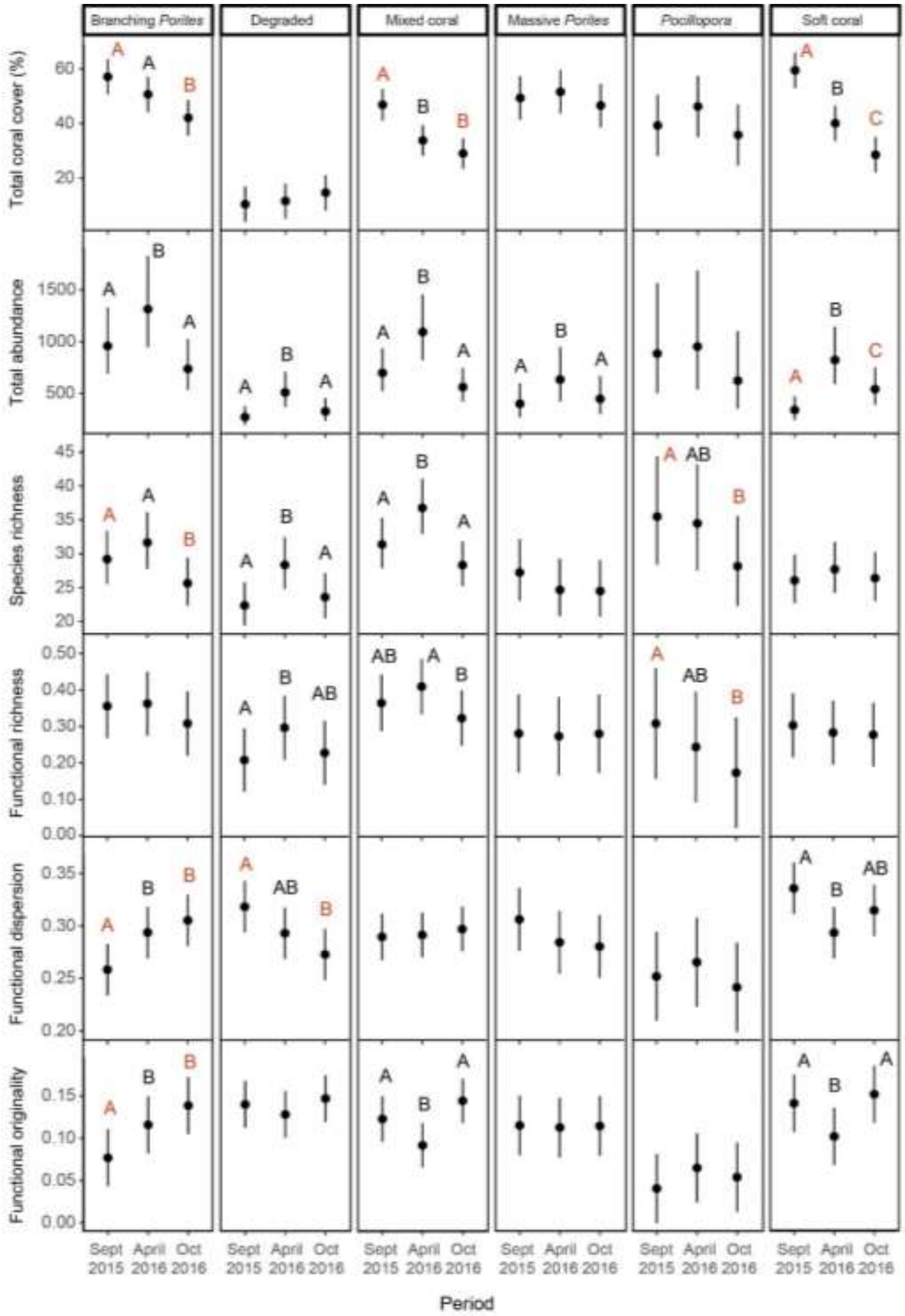

Fig. 1 Within-habitat variation (fitted values ± 95% confidence intervals) in total coral cover (%), fish species richness, total fish abundance, fish functional richness, functional dispersion, and functional originality over survey periods. Contrasting letters indicate significant planned comparisons within habitats over time (red letters highlight differences between September 2015 and October 2016).

Fish assemblage structure

The four PCoA axes cumulatively explained 56.8% of the projected inertia in the distribution of fish species traits (Fig. 2 and 3). Generally, fish body-size and mobility increased along PCoA 1 and 2, with diet groupings positioned along those gradients, ranging from small-bodied site attached farming species through to larger, more mobile, piscivorous fish species (Fig. 2). Nocturnally active, schooling planktivores occupied the left of PCoA1, and browsers were positioned in the centre of PCoA 1 and 2. Generally, species clustered more closely on PCoA 3 and 4. However, PCoA 4 separated excavating (PCoA3 left), farming (PCoA3 centre), and mixed diet feeding species (PCoA3 right), from all other species (Fig. 2).

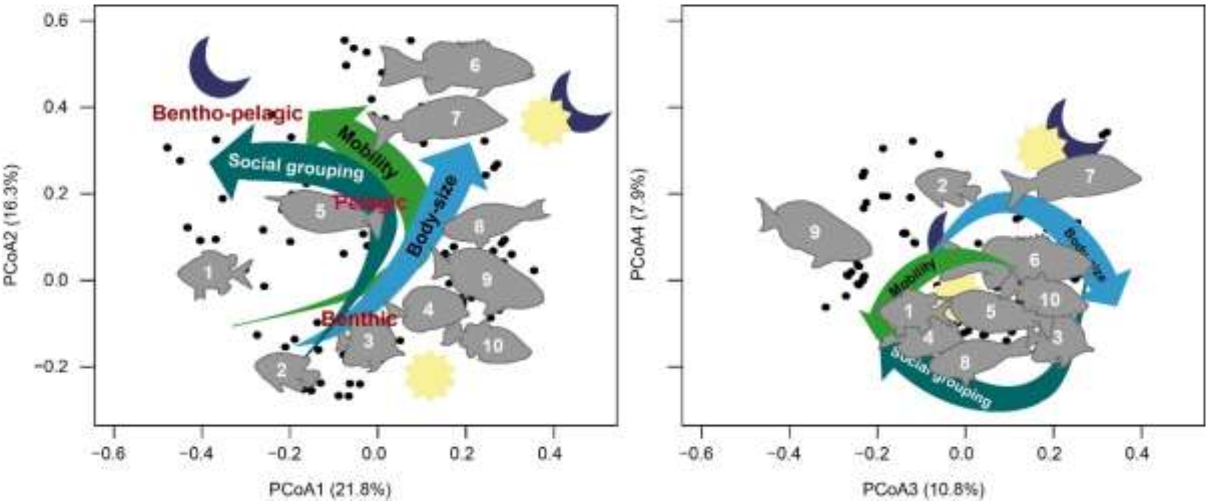

Fig. 2 Trait-based principal coordinates analysis of surveyed fish in functional space. Two hundred and seventeen surveyed fish species (black dots) plotted four dimensions of functional space defined by six traits: mean observed body-size (blue arrow indicating increasing size); diet (fish symbols: 1, planktivore; 2, farmer; 3, corallivore; 4, grazer/detritivore; 5, browser; 6, piscivore; 7, mixed diet; 8, scraper; 9, excavator; 10, invertivore); mobility (green arrow indicating increasing mobility); social grouping (dark blue arrow indicating gradient from

solitary fishes to large schools); time of activity (sun and/or moon); and position in the water column (red text). Illustrations show the average position of traits in the functional space.

Analysis of within-habitat variation in fish assemblage structure revealed changes in taxonomic (species richness and total abundance) and functional (functional richness, dispersion, and originality) characteristics in response to the bleaching event (Fig. 1 and 3). However, the nature of these changes varied among habitats (Table 2; Fig. 1; Table S5 and S6). Between September 2015 and October 2016, fish species richness declined in branching *Porites* and *Pocillopora* habitats; total fish abundance increased in soft coral habitats; functional richness declined in *Pocillopora* habitat; functional dispersion increased in branching *Porites* habitats, and decreased in degraded habitats; and functional originality increased in branching *Porites* habitats (Fig. 1 and 3).

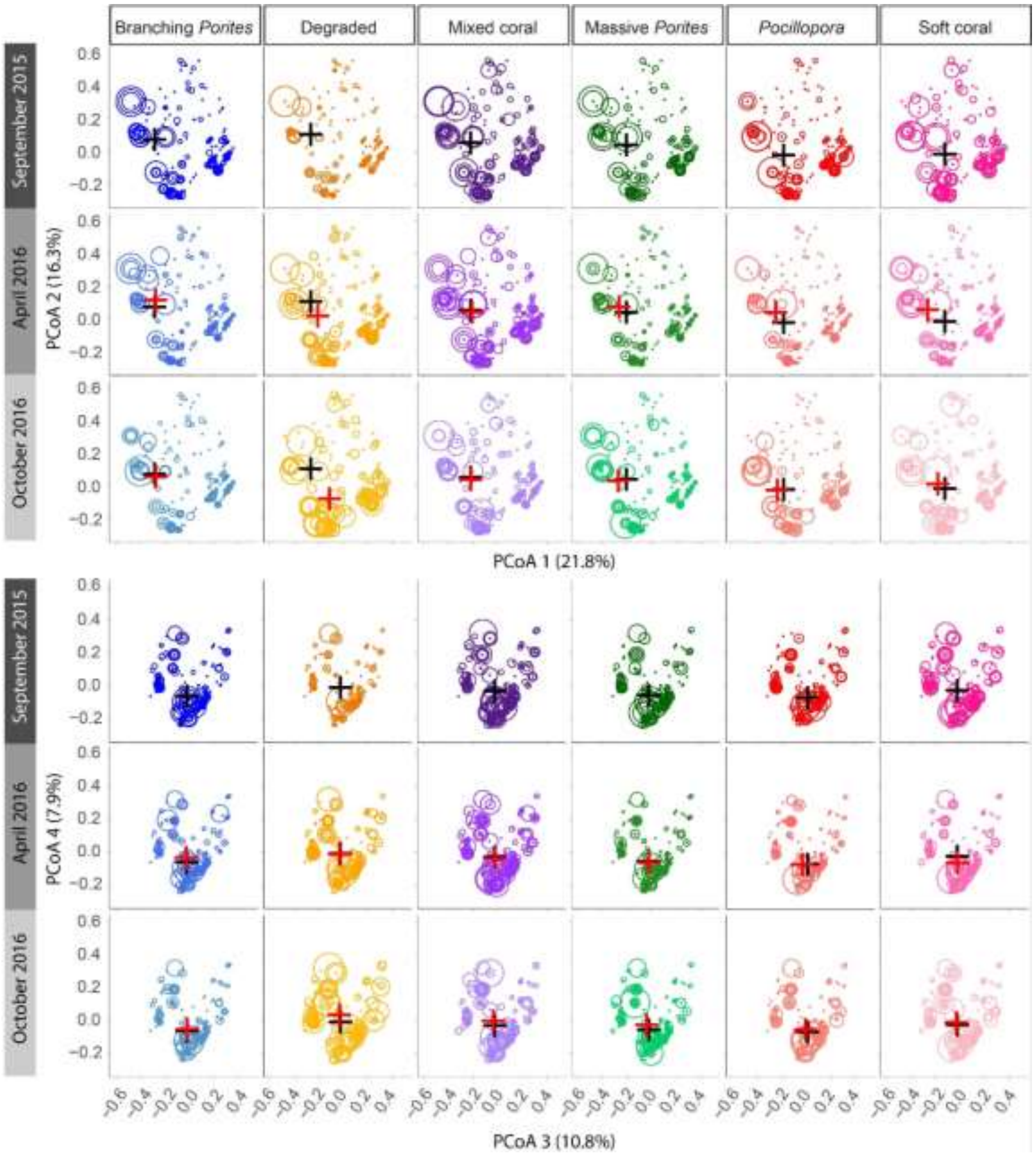

Fig. 3 Principal coordinates analyses (PCoA) of fish assemblage functional structure in habitats in each period, showing the first two (top: PCoA 1 and 2), and second two (bottom: PCoA 3 and 4), dimensions of functional trait space. Circle sizes are proportional to species mean relative abundances. Crosses mark community weighted mean centroids in each period (black: September 2015; red: April 2016, or October 2016).

Table 2 Significant planned comparisons (contrast effect size and 95% confidence intervals; CI) of within-habitat variation in total coral cover and fish assemblage responses between September 2015 and October 2016 among habitats.

Response	Habitat	Period contrast	Lower CI	Upper CI	Test stat	*df*	*P*
Total coral cover	Branching *Porites*	-15.049	-21.725	-8.373	-4.44	265	<0.001
	Mixed coral	-17.875	-23.882	-11.867	-5.86	265	<0.001
	Soft coral	-30.927	-37.603	-24.251	-9.12	265	<0.001
Fish species richness	Branching *Porites*	0.879	0.775	0.996	-2.03	266	0.04
	Pocillopora	0.793	0.648	0.972	-2.25	266	0.02
Total fish abundance	Soft coral	1.597	1.210	2.108	3.32	265	<0.001
Functional richness	*Pocillopora*	-0.135	-0.255	-0.015	-2.22	265	0.03
Functional dispersion	Branching *Porites*	0.047	0.018	0.077	3.14	265	0.002
	Degraded	-0.046	-0.075	-0.016	-3.04	265	0.003
Functional originality	Branching *Porites*	0.062	0.024	0.099	3.24	260	0.001

These changes caused an increased overall similarity in the taxonomic and functional diversity of fish assemblages across distinct habitat types. Analysis of among habitat variation in fish assemblage structure over time revealed that prior to the bleaching event there was significant variation in species richness, total fish abundance, fish functional dispersion, and functional originality, with habitat type accounting for 14–39% of the variation in these indices (not including fish abundance). Eight months after the bleaching event, however, this variation was almost entirely lost, with habitat type accounting for just 8–17%) of the variation in those measures (Table 3; Fig. 4). There was also an increased similarity in the taxonomic and functional composition of fish assemblages after the bleaching event. The number of pairwise differences in taxonomic composition among habitats declined from 7 in September 2015, to 5 in April 2016, and just 4 by October 2016 (PERMANOVAs: September 2015: Pseudo-*F* = 2.42, *df* = 5, *P* = 0.0001, all pairwise comparisons *P* <0.05; April 2016: Pseudo-*F* = 2.02, *df* = 5, *P* = 0.001, all pairwise comparisons *P* <0.05; October 2016: Pseudo-*F* = 1.94, *df* = 5, *P* = 0.001, all pairwise comparisons *P* <0.03). Similarly, the number of pairwise differences in functional composition indicated by CWMs across the four PCoA axes declined from 11 in September 2015, to two in April 2016, and 4 by October 2016 (Table 4). Changes in CWM for PCoA axes 1 and 2 indicated no changes in dominant traits across habitats though time. However, CWM values on PCoA 3 and 4 exhibited significant directional shifts overall between September 2015 and October 2016, indicated by back (September 2015) and red (October 2016) centroid cross markers, towards small-bodied habitat generalist algae-farming species (Table 4; Fig. 2 and 3).

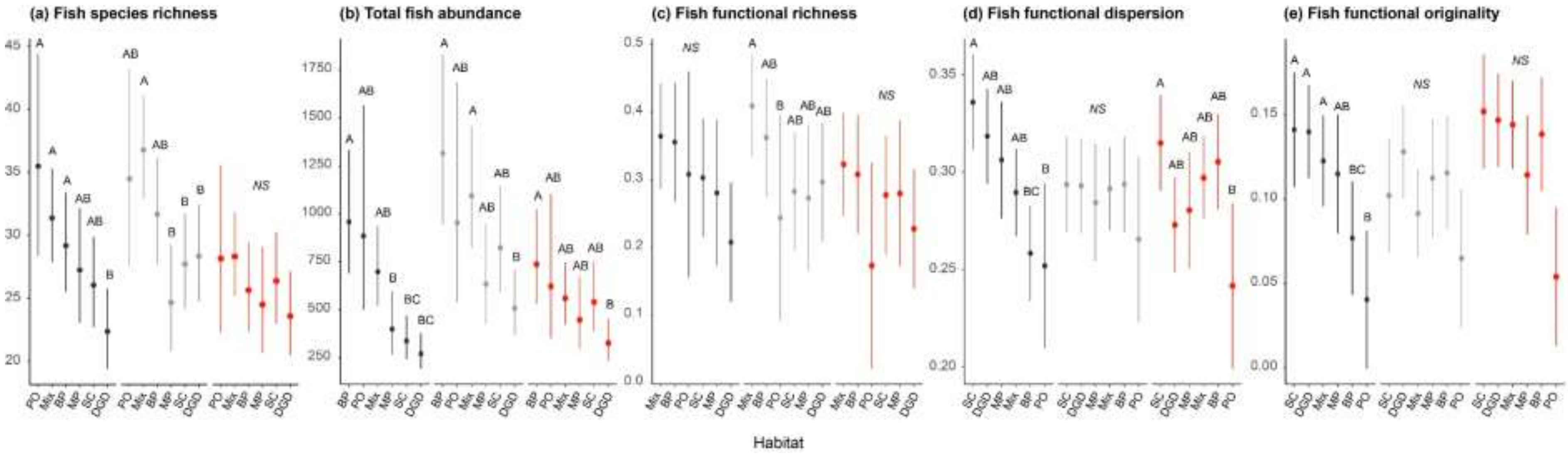

Fig. 4 Among-habitat variation in fish assemblage structure within each time-period (fitted values ± 95% confidence intervals): September 2015 (black); April 2016 (grey), and; October 2016 (red). Different letters illustrate significant differences among habitats within each period revealed by linear mixed effects models (habitat as fixed effect) and Tukey pair-wise comparisons *post hoc* (P <0.05). Habitats: BP, branching *Porites;* DGD, degraded reef; Mix, mixed coral; MP, massive *Porites*; PO, *Pocillopora*; and SC, soft coral.

Table 3 Components of variation for mixed effects models of fish assemblage structure among habitats in each survey period and Tukey multiple comparisons (number of among-habitat differences in brackets shown in bold). Habitats: BP, branching *Porites*; DGD, degraded; Mix, mixed coral; MP, massive *Porites*; PO, *Pocillopora*; SC, soft coral.

Fish response metric	Period	R^2 fixed (habitat)	R^2 random (site)	R^2 residuals (transects)	Habitat differences (P <0.05)
Species richness	Sept-15	0.28	0.11	0.61	**(3)** DGD ≠ BP, Mix, PO
	April-16	0.32	0.13	0.55	**(3)** Mix ≠ DGD, MP, SC
	Oct-16	0.08	0.22	0.69	**(0)**
Total fish abundance †	Sept-15				**(7)** BP ≠ DGD, MP, SC; Mix, PO ≠ DGD, SC
	April-16				**(2)** BP, Mix ≠ DGD
	Oct-16				**(1)** BP ≠ DGD
Functional richness	Sept-15	0.14	0.31	0.55	**(0)**
	April-16	0.23	0.13	0.64	**(1)** SC ≠ Mix
	Oct-16	0.10	0.26	0.64	**(0)**
Functional dispersion	Sept-15	0.33	0.10	0.57	**(3)** BP ≠ DGD, SC; SC ≠ PO
	April-16	0.02	0.09	0.89	**(0)**
	Oct-16	0.14	0.02	0.84	**(1)** SC ≠ PO
Functional originality	Sept-15	0.39	0.03	0.59	**(7)** BP, PO ≠ DGD, Mix, SC; PO ≠ MP
	April-16	0.04	0.05	0.91	**(0)**
	Oct-16	0.15	0.24	0.60	**(0)**

† R^2 estimations not available for generalized linear mixed models with negative binomial distribution.

Table 4 Variation in community abundance-weighted means on each PCoA axes indicating change in the functional structure of fish assemblages through time, and differences among habitats (Tukey, $P < 0.05$). The number of inter-habitat differences within each period are shown for each axis.

PCoA axis	PCoA axis inertia explained (%)	Change (Sept 2015 – Oct 2016)	Overall habitat differences	Habitat differences ($P < 0.05$)		
				Sept 2015	April 2016	Oct 2016
PCoA 1	21.8	No	BP ≠ DGD, Mix, SC	2	0	2
PCoA 2	16.3	No	BP ≠ DGD, Mix	0	2	1
PCoA 3	10.8	Yes	PO ≠ DGD	5	0	1
PCoA 4	7.9	Yes	n/a	4	0	0

Changes in fish assemblage structure across habitats between September 2015 and October 2016 were largely unrelated to levels of coral loss (Table 2; Fig. 1; Table S5). For example, in the three habitats that experienced significant coral loss, there were either no detected changes in fish assemblages (mixed coral); total abundance increased (soft coral); or species richness declined, and functional dispersion and functional originality increased (branching *Porites*) (Fig. 1; Table S6). Additionally, species- and functional richness declined in *Pocillopora* habitat, and fish functional dispersion increased in degraded habitats despite no change in coral cover (Table 2; Fig. 1). Analyses of the relative influence of coral loss on variation in all five measures of fish assemblage structure revealed total coral cover in all top candidate multiple linear regression models. However it was not the best predictor of variation in any metric (species richness, total abundance, functional richness, functional dispersion and functional originality) relative to the influence of time-period or habitat type (or their interaction; Table S7).

Discussion

Our study of the impacts of mass coral bleaching on coral reef fish assemblage structure across six taxonomically distinct reef habitats revealed three key findings. First, we show that bleaching disturbance increased the taxonomic and functional similarity of fish assemblage structure due to species turnover among previously differentiated fish assemblages (i.e., biotic homogenization). Second, we found that despite limited change in taxonomic or functional richness across all habitats, the functional originality of fish assemblages increased. This is potentially important because it suggests that there was a net loss of functional redundancy at the system level. Third, we found that pre-bleaching coral species composition was a better predictor of changes in fish assemblage structure, than absolute coral loss. These results emphasize how measures of alpha diversity (taxonomic or functional richness) can mask important changes in ecosystems as assemblages reorganize with implications for ecosystem function. Our findings also highlight the important but poorly understood role of coral species composition in structuring communities and influencing cross-scale resilience to system-wide disturbance due to the response diversity of corals and reef fishes.

The system-wide biotic homogenization among previously differentiated reef fish assemblages was evident by the increased similarity in the taxonomic and functional composition of fish assemblages following the bleaching event. Prior habitat-related differences in fish species richness, total abundance, functional dispersion, functional originality, and the taxonomic and functional composition of fish assemblages was largely lost after the bleaching event, despite no change in the taxonomic or functional richness across all surveyed reefs (local alpha diversity). Biotic homogenization is increasingly considered a central component of the broader biodiversity crisis (Olden et al., 2004; McKinney & Lockwood, 1999, McGill et al., 2015). Whilst disturbance-mediated loss of species has occurred across ecosystems (Olden et al., 2004; Butchart et al., 2010), meta-analyses show no systematic loss of species richness, rather a loss of beta diversity, suggestive of increasing biotic homogenization at a global scale (Dornelas et al., 2014). Biotic homogenization has been documented across several groups including temperate marine fishes (Magurran, Dornelas, Moyes, Gotelli, & McGill, 2015), freshwater fishes (Villéger, Grenouillet, & Brosse, 2014), birds (Cassey, Lockwood, Blackburn, & Olden, 2007), and plants (Schwartz, Thorne, & Viers, 2006; Rooney, 2009). We add to these studies with evidence of a high diversity coral reef ecosystem response to climatic disturbance, showing that isolated measures of α diversity (i.e. richness) can conceal important spatial beta diversity trends, such that the presence of species does not capture the rapid reorganisation of assemblages (Magurran et al., 2015; McGill et al., 2015).

The consequences of biotic homogenization are not yet well understood (Olden et al., 2004). However, trait-based functional approaches are increasingly used to provide insight into ecological changes that may influence the functional stability of ecosystems (Mouillot et al., 2013; Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015). We observed an increased similarity of functional dispersion (trait variability), functional originality (trait uniqueness), and functional composition of reef fish assemblages following the bleaching event. Furthermore, we found subtle but significant directional shifts in dominant fish traits across habitats towards algae-farming, small-bodied habitat generalists, causing an increased homogenization of trait space. These findings are consistent with reports of functional homogenization occurring across scales and ecosystems (Devictor, Julliard, Couvet, Lee, & Jiguet, 2007; Abadie, Machon, Muratet, & Porcher, 2011; Pool & Olden, 2012; Villéger et al., 2014). The susceptibility of a species to extirpation is typically non-random, and related to organism traits such as body-size, diet, fecundity, growth-rate, habitat specialisation, social grouping and abundance (McKinney, 1997; Graham et al., 2011). As predicted by niche theory (Hutchinson, 1957), building evidence suggests that global changes are causing worldwide declines of specialist species which have effectively been replaced by generalists thereby increasing functional similarity at the community level (Clavel et al., 2011). Indeed, severe coral bleaching events tend to favour larger-bodied, habitat generalists at the expense of obligate coral feeders and small-bodied fishes reliant on live coral habitat structure (Wilson et al., 2006; Pratchett et al., 2011). However, trait vulnerability to bleaching events can vary with the rate and extent that coral tissue mortality also leads to the loss of the physical coral structures (Wilson et al., 2006). Within the current study, coral tissue mortality caused a loss of soft coral colony structures (Ferrari 2017), but not of hard corals whose carbonate colony structures remained largely intact by October 2016. Experimental evidence suggests that soft coral exerts little direct influence on reef fish assemblages (Lewis 1998). Therefore, shifts in dominant traits from habitat specialists to generalists appear likely to result from the loss of coral tissue rather than habitat structural complexity.

Together with taxonomic and functional homogenization, we detected an increase in functional originality at the system level, inferring overall loss of functional redundancy of fish assemblages following coral bleaching, and providing further evidence of non-random trait filtering. The increase in functional originality was largely driven by species shifts in branching *Porites* habitats, where live coral tissue was lost though colony structures remained intact, and fishes with a strong preference for live branching coral (e.g. small-bodied, site-attached, schooling planktivores), were replaced by a range of other functional entities including algae-farming, habitat generalists. As habitat disturbance reduces the abundance of functionally similar species, the number of species contributing to any one function (i.e., functional redundancy) may decline as remaining species become relatively more functionally unique (Walker, 1992; Reich et al., 2012). We found that trait-filtering of habitat specialists likely reduced the competitive exclusion of other functional entities, facilitating habitat use by a range of other groups and reducing functional redundancy at the community level (Macarthur & Levins, 1967). We provide clear data showing that whilst functional richness remained consistent across the bleaching event, the turnover of fish species altered the distribution of traits in specific habitats. However, changes were poorly predicted by the loss of coral at the system level.

Interestingly, pre-bleaching coral species composition was a better predictor of changes in fish assemblage structure following the bleaching event than the specific level of coral loss within each habitat type. Whilst substantial coral loss typically incurs concurrent declines in the species richness and total abundance of reef fishes after bleaching (>20% total cover and reduction in absolute cover below 10%; Wilson et al., 2006), we show that observed changes in fish assemblage structure (including species richness and total abundance) were variable among habitats and inconsistent with changes in coral cover. For example, the greatest changes in fish assemblage structure occurred in branching *Porites* habitats that lost 15% coral cover. However, in mixed and soft coral habitats that experienced greater coral loss (18% and 31%, respectively), fish assemblage structure only changed in soft coral habitats (the only habitat where the physical coral structures were also lost) where total fish abundance increased. Further, changes in fish assemblage structure were evident in habitats where significant coral loss was not detected (e.g. reduced taxonomic and functional richness in *Pocillopora* habitat). With widespread coral bleaching across habitats, our results illustrate the differential susceptibility of distinct reef fish assemblages, governed primarily by the vulnerability of particular fish traits associated with specific coral configurations. Coral habitats provide a range of niche spaces for the coexistence of diverse but functionally unbalanced fish assemblages (Mouillot et al., 2014; Brandl, Emslie, Ceccarelli, & Richards, 2016; Richardson, Graham, & Hoey, 2017). Some provide particular niche habitat to specialist guilds of fishes (Richardson, Graham, Pratchett, et al., 2017), such that relatively small habitat disturbance may incur disproportionate change in fish assemblage structure. Indeed, we found that fish assemblages in branching coral habitats (branching *Porites* and *Pocillopora*) were most negatively impacted by the bleaching event, despite differential coral loss. Conversely, coral reefs with high or diverse initial coral cover that incur coral loss may have limited effects on fish populations if the availability of required habitat remains sufficient (e.g. corallivores, Pratchett, Wilson, & Baird, 2006), such as in mixed coral habitats in our study.

These results provide some insight into the underlying dynamics of coral bleaching on reef fish assemblages, and highlight the role of coral species composition in determining the susceptibility of assemblage structure to disturbance. However, further examination of coral habitats across locations, particularly reefs characterised by dominant though thermally sensitive *Acropora*, would enable better understanding of how shifts in coral species composition may affect changes in fish assemblage structure at a broader scale. Furthermore, our results only provide a snapshot of a highly complex, dynamic system, and caution is recommended for applying these findings to longer-term predictions. It is unknown if the observed functional trait shifts constitute a temporary phase in the reassembly of coral reefs directly following acute bleaching disturbance, or if shifts will be sustained (Bellwood et al., 2012). Similarly, lag-responses to bleaching events have been observed in corals (e.g. disease; Bruno et al., 2007; Miller et al., 2009), and populations of coral reef fishes where the delayed erosion of dead coral structures has caused substantial declines in smaller size-classes of reef fish (Wilson et al., 2006; Graham et al., 2007). There is much uncertainty about how distinct and emerging configurations of species will respond to ongoing disturbances and how important ecosystem processes will be maintained (Graham et al., 2014). A great deal more research is needed in this area to understand reef dynamics in the Anthropocene, so to guide viable and pragmatic management approaches (Norström et al., 2016). Finally, whilst trait-based estimations of ecological diversity provide a useful tool for assessing the functional trajectory of disturbed ecosystems, we acknowledge that they remain coarse approximations based on our current understanding of species' roles that do not likely capture finer-scale, nuanced niche partitioning (McGill, Enquist, Weiher, & Westoby, 2006).

Climate induced mass coral bleaching often devastates coral reef ecosystems, threatening the livelihoods of people that rely upon the ecosystem services that reefs provide (Moberg & Folke, 1999; Norström et al., 2016). As global temperatures rise, new governance challenges are faced by managers as non-random species shifts transform reef assemblages into novel configurations of species (Graham et al., 2014), with unknown implications for their capacity to maintain key ecosystem functions (Norström et al., 2016; Hughes, Barnes, et al., 2017). Comparing the impacts of bleaching on reef fish assemblage structure across distinct reef habitats provided some insight into the variable responses of both corals and fishes to thermal stress, and highlighted the potential homogenization of fish assemblages across scales. Biotic homogenization is increasingly considered one of the most pressing, but largely unrecognized, biodiversity crises faced globally (Dornelas et al., 2014; Magurran et al., 2015; McGill et al., 2015). Our results underscore the importance of coral species composition in determining ecological organisation and the susceptibility of reef ecosystems to disturbance. As species shifts persist, the suitability of coral reef management and the value of different coral dominated states will likely hinge upon the capacity of those ecosystems to maintain key ecological processes with ongoing disturbance.

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